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BIOLOGICAL BASES FOR THE MANAGEMENT OF LESSONIA NIGRESCENS (PHAEOPHYTA, LAMINARIALES) IN CENTRAL CHILE

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INTRODUCTION

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Biologically speaking, Lessonia nigrescens is the most important brown alga in the intertidal zone of the Chilean coast (Santelices et al., 1980). The species is found from Callao, in central Peru, to Cabo de Hornos at the southernmost tip of Chile (Taylor, 1947; Levring, 1960; Dawson et al., 1964) and is the dominant intertidal species in terms of cover and biomass all along this coast.

*Numbers in the right-hand margin indicate the corresponding page in the original. Abstract on page 32.

Since 1975 the species Lessonia nigrescens has taken on growing economic importance in Chile as a source of alginates. Exports of 300 dry tons in 1975 had risen to 6000 dry tons by 1979 (Joyce and Santelices, 1978, Santelices and Lopehandía, 1981) . Lessonia nigrescens was harvested in 1978 and 1979 from Los Vilos to Arica, an area ranging from about 17°S to 30°S. Those volumes dropped in 1980 and 1981 south of 25°S, but intensive harvesting continues north of that latitude (National Fisheries Service, 1981).

Because of the dominance of Lessonia nigrescens in rocky intertidal areas and the considerable size attained by its plants (up to 4 m long), this alga serves as the habitat for and apparently determines the presence and abundance of numerous other intertidal organisms. Most conspicuous perhaps are the many taxa of invertebrates sheltered within the holdfast, safe from predators and wave action (Cancino and Santelices, 1981). Hence, the removal of Lessonia nigrescens may jeopardize not only the population structure of the alga but also the structure of intertidal invertebrate communities living in and among the holdfasts of this species.

Little attention has been given to the biology of the species, despite its indisputable ecological importance and growing economic potential. Although some work has been done on systematics and morphology (Taylor, 1947; Searles, 1978) and the early development of the species has been described in some detail (Olivari, 1972, 1974; Hoffmann and Santelices, 1982), practically no information is available on its production ecology or interaction with other organisms. The extensive literature on other Laminariales of ecological and economic importance elsewhere in the world

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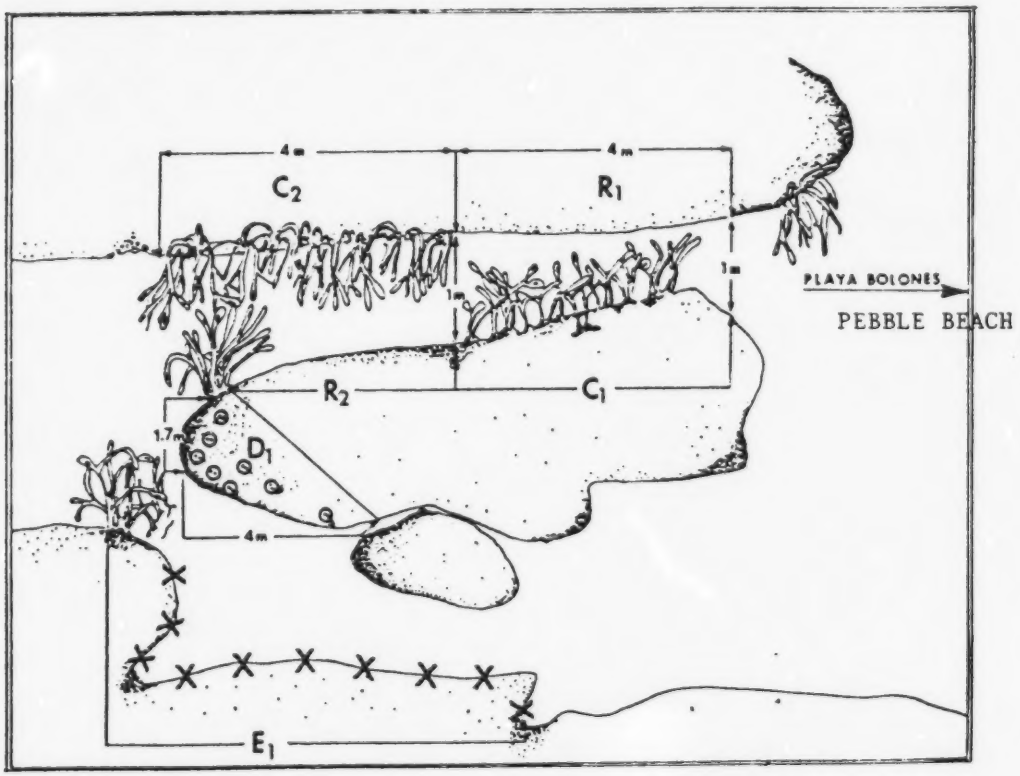
(see for example revisions of Kain, 1971 and North, 1971) cannot be readily extrapolated to Lessonia nigrescens, because of marked morphological and ecological differences between Lessonia nigrescens and other Laminariales, and because of the unique biogeographical features and the isolation of associated intertidal flora on the coast of Chile (Santelices, 1980). Accordingly, our objective was to obtain the basic biological data required to design a management plan for this species in central Chile. More specifically, our research addressed the following three aims:



MAP - LOS MOLLES STUDY AREA

Figure 1.- Map of experimental site at Los Molles. R_1 and R_2: areas from which Lessonia nigrescens was removed. D_1: plants pruned at holdfast level. E_1: plants pruned at first dichotomy. C_1 and C_2: control areas.

1) Determination of optimal harvesting season, based on periodicity of growth, reproduction, juvenile settlement and gel production in this species.

2) Determination of size of plant to be harvested, based on size of reproductive plants, changes in invertebrate community structure over time and weight accumulated by the plant.

...

(Tr. Note: lines missing in original)

... of the plant determined by spatial distribution patterns of gels in the plant, its post-pruning regeneration capacity, and the effect of its removal on other intertidal organisms and particularly on juvenile recruitment.

MATERIALS AND METHODS

Research site: All of the observations, measurements and experiments described in this study were carried out at Los Molles Cove ($32^{o}10'S$), an area of exposed rocky platforms and troughs which it was possible to examine only during low tide, and which are inaccessible to fisherman and visitors to the beach. Two types of habitat were distinguished here: rocky platforms and pebble beaches. The seven study areas marked off on the platforms are shown in Figure 1. In May of 1980, the entire Lessonia nigrescens population (50 individuals) was removed from two of these areas (R_1 and R_2). In two adjacent areas ... . (lines missing in original) .... undisturbed as controls. In each of these areas 25 representative plants were tagged for growth measurement purposes.

In a third experimental area called D, located close to the other two, all the stipes of each plant were severed 1-2 cm from the holdfast. Finally, plants in a fourth experimental zone called E_1 were pruned at the first dichotomy.

Morphometric ratios: Morphometric relationships were examined in the 50 individuals removed in May of 1980 from areas R_1 and R_2. The plants were taken in separate plastic bags to the laboratory, where 13 morphometric and gravimetric characters were measured (Table 1).

TABLE 1.- Morphometric ratios studied in Lessonia nigrescens populations

HOLDFAST

Disc height/disc diameter at broadest point
Narrowest disc diameter/broadest disc diameter

STIPES

- Stipe length/basal diameter of stipes
- Stipe weight/basal diameter of stipes
- Stipe weight/stipe length
- Length from attachment disc to first dichotomy/stipe length
- Length from attachment disc to first dichotomy/basal diameter of stipe
- Number of dichotomies/stipe length
- Stipe weight/number of dichotomies
- Number of dichotomies/length to first dichotomy

HOLDFAST/STIPES AND BLADES

Disc weight/weight of blades and stipes
Total plant weight/disc diameter at broadest point
Number of stipes/broadest disc diameter

Growth and reproductive periodicity: Control plants in areas C_1 and C_2 were used to study growth and reproductive periodicity. One stipe selected at random was tagged on each of 25 Lessonia nigrescens plants in each area. Each month, from May 1980 to June 1981, changes in the following morphological characters was measured for each individual: height, diameter of the anchoring disc at the broadest and narrowest points, total number of stipes per plant and number of reproductive stipes, length and broadest diameter of tagged stipes, length from disc to first dichotomy of the stipe and total number of dichotomies on the stipe.

In the pebbled area, some 20 m from the rocky platform site, a further 50 plants were tagged in order to record the same morphological changes. Three plants were also chosen in this area for the measurement of growth in all stipes.

In order to ascertain the timing of juvenile settlement, areas R_1 and R_2 were kept clear of large grazers, particularly sea urchins (Tetrapygus niger) and chitons (Acanthopleura echinata). The first juvenile settlements were recorded in August 1980. In September 1980, 100 of these individuals were tagged to measure their growth rate relative to the characteristics and sizes mentioned previously. This study continued until December 1981.

Gel analysis: The gel content of five different parts of Lessonia nigrescens individuals was analyzed monthly: holdfast, stipes to the first dichotomy, stipes above the first dichotomy, sterile fronds and reproductive fronds.

Our decision to distinguish between stipes below and above the first dichotomy was related to the different pruning strategies being tested in the field.

The plants analyzed were collected in the vicinity of the experimental areas in the platform sector. Each month, from May 1980 to June 1981, five plants were collected, sectioned and weighed in the field. Epiphytes and other impurities were removed in the laboratory, where the material was desalinated in fresh water and oven-dried at 70°C to constant dry weight. Twenty grams of dry material were then digested for one hour in 1,000 cc of calcium carbonate solution. The algae were then well dampened and ground in a blender, and the material was cooked for 4 hours in 90°C water. This produced hydrolysis of the gel, which was then filtered through diatomaceous earth using a specially-designed pressure pump and compressed air. Calcium hydroxide was added to the filtrate to precipitate the gel in the form of calcium alginate, which was then converted to alginic acid, lowering the pH of the medium with a hydrochloric acid solution. The alginic acid was then dried to constant temperature and weighed to calculate the final extract as a percentage of original dry weight. 139

Holdfast community structure: A preliminary picture of the distribution, abundance and diversity of invertebrates inhabiting different sizes of Lessonia nigrescens attachment discs emerged after an examination of the holdfasts of the 50 plants taken from experimentally cleared areas (R_1 and R_2, Fig. 1). A series of basal relationships characterizing these invertebrate colonies was then determined. Additionally, three discs

were collected every three months from the control area (C_1, C_2, Fig. 1), in order to assess seasonal variations in the structure of this community.

The holdfasts to be removed from their natural habitat were surrounded by plastic bags and scraped from the substrate using metal bars. The animals were gathered directly into the plastic bag as the disc was being lifted, and the disc was placed in the same bag, numbered and taken to the laboratory for further study. In the laboratory, tweezers were used to remove the larger animals, while the smaller invertebrates had to be obtained by dissecting the holdfast under a stereoscopic microscope. The invertebrates were identified, separated by species, sexed and weighed. Quantitative relationships between invertebrate species and between the invertebrates and the holdfast were processed by a DEC System Computer at the Computer Centre of the Pontificia Universidad Católica de Chile, using the University of Western Michigan "Bank" and "STP" statistics packages.

Evaluation of pruning systems: All stipes of each plant in study area D_1 were severed 1-2 cm from the disc. All stipes removed from each plant were placed in separate plastic bags for subsequent laboratory analysis. Each disc pruned in the field was measured (height, diameter at broadest and narrowest points), the number of stipes counted and the holdfast tagged with a plastic marker. Thirty discs were tagged in all, with diameters ranging from 4 to 30 cm. In another experimental area (E_1, Fig. 1) 20 plants were pruned at the first dichotomy and three stipes chosen at random were tagged in each plant.

Pruned and control plants at both experimental sites were tagged and their discs measured monthly; where applicable, the length from the holdfast to the first dichotomy was recorded as well. Every three months three complete representative plants of each of the two experimental pruning systems were removed from the substrate and processed in the laboratory for gel extraction and an examination of the invertebrates in the disc, as described earlier for the control plants.

This working schedule was maintained from May 1980 to June 1981. However, in about December 1981 it became evident that more analysis was required of the effect of adult Lessonia nigrescens plants and grazers on the settlement of juveniles of this kelp species. To this end, four experimental plots each 12 m^2 were marked off in the pebble beach area. Two of the areas were cleared of all Lessonia nigrescens plants. A total of 200 Tetrapygus niger individuals were added at one site, kept in by the large algae bordering the 12 m^2 site. No sea urchins were added to the second plot, which was kept clear of those animals and of adult plants. The third area was left undisturbed as a control, and the fourth was partially cleared of plants, in order to study the recolonization capacity of Lessonia nigrescens when stands are thinned to leave maximum interplant distances of up to 2 m. The first three experimental plots were prepared in January 1981, the fourth the following June. They were maintained until November of 1981, with monthly records kept in each of the number of juveniles settling and average maximum thallus length, using a representative population of 30 individuals collected at random.

RESULTS AND DISCUSSION

1.- Determination of optimal harvesting season

Figure 2 summarizes the data most useful in identifying the optimal harvesting season for this species in central Chile. Information is included on seasonal variation in growth, reproduction and gel content of the species.

a) Growth patterns:

The growth rate of tagged Lessonia nigrescens populations was measured taking into consideration several plant characters, namely stipe length, length from attachment disc to first dichotomy, broadest holdfast diameter and stipe number. Figure 2 shows the seasonal variation in the length of tagged stipes of these plants, a variation pattern which is representative of the other morphometric characteristics measured. Between June 1980 and May 1981, average stipe length increased by 145% ($\bar{x}$ = 12.1% monthly). Growth was fastest in the winter months and in early spring (August-October). During late spring and summer stipe length increases slowed, in apparent response to two phenomena: destruction of the scar tissue after release of spores, and dehydration and discoloration as a result of low tides during the hours of the day when sunlight is most intense and temperatures highest. Discoloured stipes which had died in these circumstances were observed frequently in the field during this period.

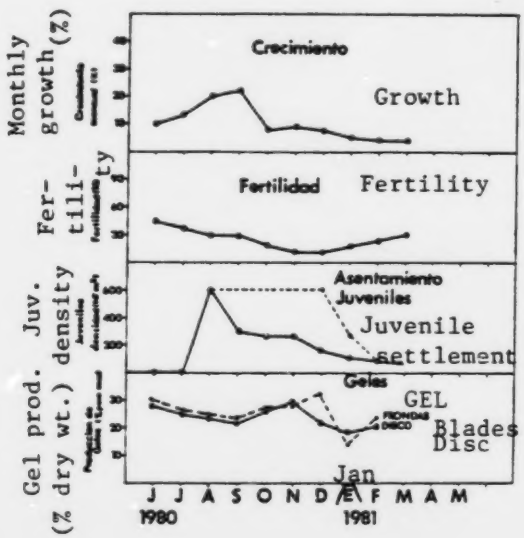


Figure 2.- Seasonal changes in growth rate, fertility and gel production in Lessonia nigrescens populations in central Chile.

b) Reproductive periodicity:

A count of the number of reproductive stipes found each month among the total tagged plants showed clear seasonal variation in spore production, with maximum values (largest number of stipes) between March and July and decreased fertility between August and February.

Juvenile settlement also followed a marked seasonal pattern. No juvenile plants were found on the rocky platforms from February to July, but they were abundant in August (Fig. 2), only to decline again from September on. This drop in individual numbers was accompanied by a marked increase

in average plant size, in what appeared to be a case of intraspecific competition.

Juveniles continued to appear at sites with available substrates until December. When the substrate was cleared experimentally at any time between August and December, it was rapidly taken over by juvenile Lessonia nigrescens plants, particularly in areas from which intense wave action had removed the older plants.

c) Seasonal variation in gel content:

Clear seasonal variations were recorded in the gel content of attachment discs, with peaks in spring and in autumn. Blades were also richest in gel in autumn and late spring. A sharp drop was noted in both parts of the plant in November, December and January. The period from September to December would thus appear to be the best months for the harvesting of Lessonia nigrescens on the coast of central Chile, as the species has by then reached peak growth and fertility values. This period coincides as well with the appearance of juveniles, which can colonize the substrate freed up by the removal of older plants. Finally, the high gel content of the plants during those months should ensure better prices for the crop.

2.- Determination of size of plants for harvesting

a) Morphometric relationships:

The holdfast diameter at its broadest point correlates positively and significantly with total plant weight (Fig. 3), since stipe production and

plant weight increase with disc size. The broadest disc diameter also correlates with weight, height and narrowest diameter of the anchoring disc, confirming the steady and balanced development of that attachment organ. Stipe weight increases logarithmically with stipe diameter and length. As the stipe lengthens, its diameter increases, as does the length from the holdfast to the first dichotomy and the number of dichotomies in stipes up to a maximum length of 280 cm. From this whole set of morphometric relationships we can deduce that the diameter of the holdfast of this species at the broadest point is an indicator of plant weight and total size, and can be applied, for that reason, in management strategies.

b) Size of reproductive plants:

Although fertility measurements show that the minimum size for fertile plants is 1.5 m, fertile sori were observed in May-June 1981 in some 20% of the juveniles which had settled in the experimental removal areas between August and November of 1980; those months in 1981 coincided with the onset of the reproductive season in the adult Lessonia nigrescens population. Average juvenile length at that time was 118 cm. The survival rate of spores produced by these plants and germination percentages are, however, significantly lower than for older plants. Thus, even though a percentage of the juvenile population can produce spores during their first year of life, this phenomenon is not generalized, and germination percentages for such spores are lower than for normal plants.

c) Invertebrate communities in Lessonia nigrescens holdfasts:

Table 2 lists the 45 species of invertebrates identified in holdfast discs of Lessonia nigrescens. Numerous representatives of four invertebrate groups were also found (Amphipoda, Nemertea, Polychaeta and Sponges), which await further study before individual species can be identified.

Table 3 is a correlation matrix depicting the relationship between the fauna found in Lessonia nigrescens holdfasts and morphometric parameters of the disc. Most of the correlations are statistically significant, indicating regular growth of the holdfast and steady, balanced growth of the holdfast relative to the number and diversity of invertebrates sheltered there. Of special interest for predictive purposes are the relationships between number of invertebrate species and disc diameter at the broadest point.

Figure 3 shows increases in numbers of individuals by species and increases in numbers of species with increases in disc diameter. The levelling off of the species number curve suggests saturation in the number of species which Lessonia nigrescens discs can support and the maximum invertebrate biomass which can be sheltered there.

TABLE 2.- Taxa found in *Lessonia nigrescens* holdfasts

Phylum Mollusca
- Class Gastropoda
  - * *Tegula atra*
  - * *Tegula tridentata*
  - *Concholepas concholepas*
  - *Scurria scurra*
  - *Crepipatella dilatata*
  - *Fisurella spp.*
  - *Diloma nigerrima*
  - * *Siphonaria lessoni*
  - *Prisogaster niger*
- Class Pelecipoda
  - *Brachidontes granulata*
  - *Semimytilus algosus*
  - *Aulacomya ater*
- Class Poliplacophora
  - * *Chiton cumingsi*
  - * *Tonicia sp.*
  - * *Chaetopleura peruviana*
  - *Acanthopleura echinata*
  - *Callistochiton viviparus*
  - *Chiton granosus*

Phylum Arthropoda
- Class Crustacea
  - *Allopetrolisthes angulosus*
  - *Allopetrolisthes punctatus*
  - *Petrolisthes violaceus*
  - *Petrolisthes tuberculatus*
  - * *Liopetrolisthes mitra*
  - *Pilumnoides perlatus*
  - * *Pisoides edwardsi*
  - *Sinalpheus spinifrons*
  - *Amphoroidea typa*
  - *Pachicheles grossimanus*
  - *Pachicheles chilensis*
  - * *Taliepus dentatus*
  - * *Homalaspis plana*
  - *Gaudichaudia gaudichaudii*
  - *Acanthocyclus sp.*
  - *Austromegabalanus psittacus*
  - *Notobalanus psittacus*
  - * *Chthamalus scabrosus*
  - * *Pagurus sp.*
- Class Amphipoda
  - Amphipoda

Phylum Echinodermata
- Class Asteroidea
  - *Patria chilensis*
  - * *Stichaster striatus*
  - * *Heliaster helianthus*
- Class Echinoidea
  - *Tetrapygus niger*
  - * *Loxechinus albus*

Phylum Chordata
- Class Ascidiacea
  - *Pyura chilensis*

Phylum Coelenterata
- Class Anthozoa
  - *Phymactis clematis*
  - *Anthothoe chilensis*

Other groups
- Nemertea
- Polychaeta
- Sponges

N = 85 holdfasts examined
Note: 45 species
4 groups
*Species represented by fewer than 4 individuals in sample.

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TABLE 3.- Correlation matrix between fauna of Lessonia nigrescens holdfasts and morphometric characters of attachment disc.

1)	Peso total	1.000								
2)	Volum. disco	0.9901	1.000							
3)	Diám. mayor	0.8845	0.8800	1.000						
4)	Diám. menor	0.8867	0.9024	0.9629	1.000					
5)	Alto disco	0.8589	0.8830	0.9201	0.9454	1.000				
6)	Nº especies	0.7525	0.7608	0.8589	0.8539	0.8355	1.000			
7)	Nº individuos	0.8126	0.8139	0.7808	0.8282	0.7364	0.8009	1.000		
8)	Biomasa invert.	0.7623	0.7606	0.7060	0.7662	0.6623	0.8083	0.9502	1.000	
9)	Nº indiv. x esp.	0.6919	0.6923	0.6649	0.7005	0.6335	0.4687	0.7819	0.6251	1.000
10)	Peso x indiv.	0.7653	0.7675	0.7698	0.7868	0.7930	0.8038	0.5844	0.6628	0.3595	1.000
11)	Log. Nº especies	0.7002	0.7067	0.8332	0.8122	0.8145	0.9228	0.6626	0.6264	0.3851	0.7492
		Peso Total	Volum. disco	Diám. mayor disco	Diám. menor disco	Alto disco	Nº especies	Nº individ.	Biom. invert.	Nº ind. x esp.	Peso x ind.
		1)	2)	3)	4)	5)	6)	7)	8)	9)	10)

1) Total weight
2) Disc volume
3) Broadest diameter
4) Narrowest diameter
5) Disc height
6) Number of species
7) Number of individuals
8) Invertebrate biomass
9) No. individuals per species
10) Weight per individual
11) Log. number of species

Also illustrated in Figure 3 is the relationship between disc diameter at the broadest point (D_1) and total number of individuals. The number of invertebrates found in the disc increases exponentially with disc size. It is interesting to note that the average weight of invertebrates in these discs is less than 100 mg. However, this average increases in larger discs, which tend to support heavier animals; this would seem to suggest that invertebrates grow inside the disc or that smaller animals are replaced by larger ones as the disc grows.

This increase in number and average weight of invertebrates with holdfast size greatly weakens the disc's resistance to the tug of the waves, and eventually the plant slips off the rock and drifts away. A sharp increase in invertebrate numbers occurs in plants having a disc diameter at the broadest point in excess of 20 cm, which would normally weigh at least 10 kg and have stipes considerably longer than 1.5 m. The plant thus has reproduced at least once. The aforesaid diameter thus appears to be a conservative cut-off point below which plants could not be harvested without jeopardizing the diversity of invertebrate life in their midst. In practical terms, the removal of such plants from their intertidal habitat simply anticipates the detachment that would ultimately follow naturally as increasing numbers of invertebrate invaders progressively weakened their anchoring capability.

d) Invasion of the holdfast:

Colonies of invertebrates inside Lessonia nigrescens holdfasts vary with the size of the disc. A classification of communities can thus be based on holdfast size, and a comparison made of the types of fauna found in different discs. Discs can be grouped according to the greater or lesser degree of similarity of their invertebrate colonies, and the invasion of their holdfasts by such fauna can be studied. Presumably, holdfasts sheltering similar fauna should form into groups. If the holdfast has been invaded gradually by species, no abrupt changes should be detected between different holdfast groups. If, however, significant changes are noted in invertebrate make-up of discs as they grow, it will be possible to identify conspicuous groups of discs characterized by a very few species.

The disc pattern shown in Figure 3 reflecting different degrees of faunal similarity forms five groups connected different similarity. An analysis of the discs shows that each of these groups corresponds to a different size of holdfast, housing a different assemblage of organisms (Table 4). The faunal make-up of these groups of discs is strongly influenced by very few but abundant species. The occurrence and relative importance of these species in different disc groups is summarized in Table 5. Semimytilus algosus and Brachidontes granulata are among the first invertebrates to invade the disc, in which they remain, at times with significantly high frequencies. Polychaeta are present in the second group of discs but not in the first, while the numbers of Phymactis clematis and Scurria scurra are high in holdfasts of the third group. The rest of the 14 species listed in Table 4 are abundant and of ecological interest only in the larger discs, corresponding to groups 4 and 5. Most of the last species in Table 4 and 5 are motile animals, for several of which the holdfast serves as a temporary habitat. Several are predatory species which, to some extent, influence and probably limit the populations of other invertebrates in the holdfast.

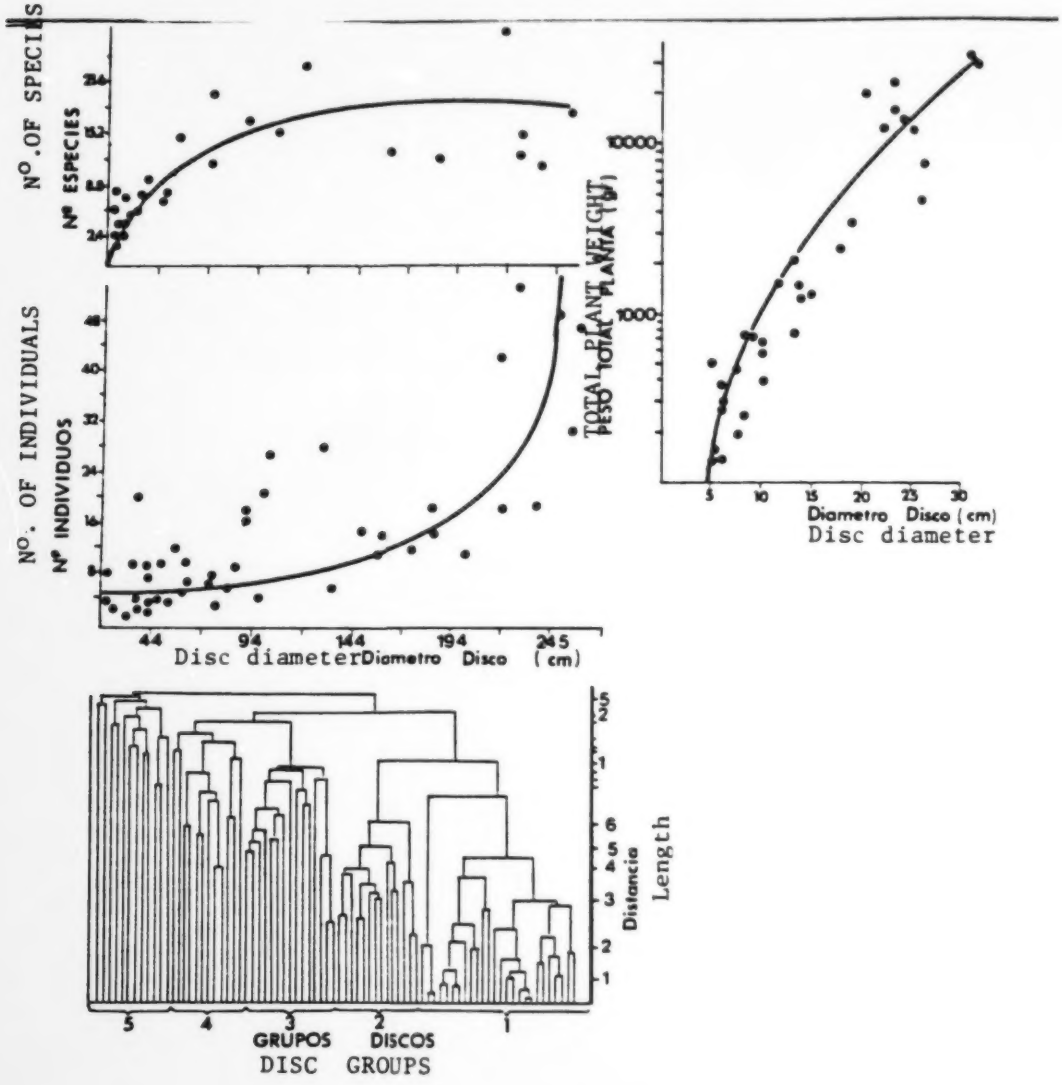

FIGURE 3.- Morphometric relationships of disc with invertebrates in L.nigrescens and cluster diagram of discs of different sizes, used to determine minimum pruning size. See text for further information.

Taken overall, these data indicate that the invasion of Lessonia nigrescens holdfasts by invertebrates is a continual species assemblage process, not the gradual replacement of certain species by others. No matter what the size of the disc removed, the fauna sheltered there will be affected in some measure, since the holdfast serves as a habitat up to very advanced stages in the plant's life. However, the invertebrates most often found in the larger discs (over 20 cm in diameter) are motile animals who use the disc temporarily.

Morphometric data on growth and fertility of invertebrate community structure in holdfast interiors and the assemblage of invertebrate species in the disc show that the minimum size of plant that should be removed has a diameter of 20-25 cm at the broadest point. This type of plant has been in the intertidal system for more than two years, and has produced spores at least twice. The holdfasts contain members of all of the invertebrate species normally sheltered there. The next step normally for such plants is a rapid increase in invertebrate density within the holdfast, the rapid erosion of the disc, and ultimately the loss of the plant.

3.- Development of a Pruning Strategy

a) Plants pruned near the disc:

The first reaction recorded in the 36 plants pruned 1-2 cm above the holdfast was a change in disc colour to dark brown. These discs were soon colonized by other algae, some ephemeral and opportunistic. Three to four

months into the experiment, these discs were found to be totally covered with epiphytes. In many cases the attachment disc had rotted, slipped off the rocks and disappeared.

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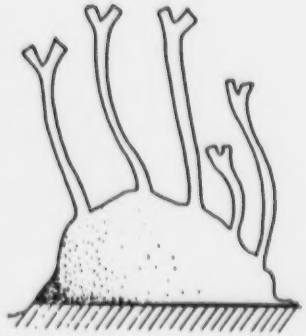
TABLE 4.- List of species, in descending order of abundance, in *Lessonia nigrescens* holdfasts (number of individuals per disc)

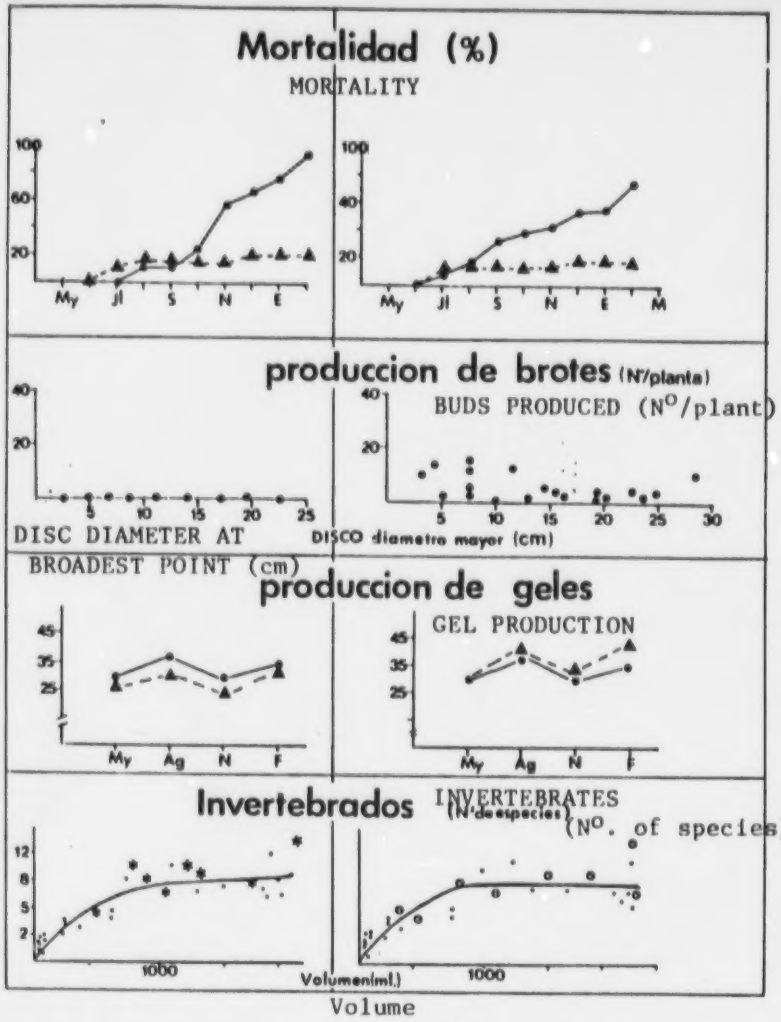
Ranking	Species	Average no. of individuals/disc
(1)	*Semimytilus algosus*	47.44
(2)	*Brachidontes granulata*	38.97
(3)	*Phymactis clematis*	16.29
(4)	*Pachicheles grossimanus*	4.99
(5)	Polychaeta	4.78
(6)	Amphipoda	4.65
(7)	*Petrolisthes tuberculatus*	4.19
(8)	*Scurria scurra*	1.62
(9)	*Acanthocyclus sp.*	1.52
(10)	*Allopetrolisthes angulosus*	1.06
(11)	*Allopetrolisthes punctatus*	1.03
(12)	*Austromegabalanus psittacus*	0.68
(13)	*Crepipatella dilatata*	0.58
(14)	*Diloma nigerrima*	0.53

TABLE 5.- List, in descending order, of invertebrates with greatest biomass in Lessonia nigrescens holdfasts (average fresh weight per disc in grams)

Ranking	Species	Average wet biomass per disc
(1)	Pachycheles grossimanus	15.277
(2)	Allopetrolisthes punctatus	5.823
(3)	Semimytilus algosus	2.309
(4)	Brachidontes granulata	2.276
(5)	Concholepas concholepas	2.050
(6)	Scurria scurra	1.958
(7)	Acanthocyclus sp.	1.283
(8)	Phymactis clematis	1.237
(9)	Petrolisthes tuberculatus	0.635
(10)	Acanthopleura echinata	0.522
(11)	Polychaeta	0.394
(12)	Allopetrolisthes angulosus	0,307
(13)	Pyura chilensis	0,277
(14)	Austromegabalanus psittacus	0,250

In terms of mortality (the removal of individuals from their rocky habitat through natural causes), Figure 4 shows that 11 months after the experimental pruning, all plants had been lost. The mortality of the control population in that same period is significantly lower (21%). In a limited number of cases, particularly involving holdfasts with smaller diameters, new blades grew from natural buds which appeared at the outer edge of the disc. Generally speaking, the pruned disc's budding capacity varies inversely with its size. Buds on the holdfast soon thickened and a small frond appeared, and the disc eventually began to grow and develop normally again. It is not surprising, then, that the only discs to grow during the pruning experiment months were several of the smaller ones. These plants eventually dry out, succumb to sea urchin attacks, and are lost. (146)





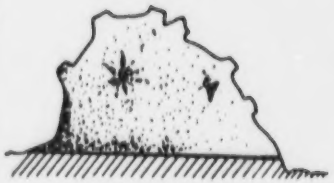


Figure 4.- Comparison of mortality, regeneration, gel production and invertebrate community structure in Lessonia nigrescens plants subjected to two different pruning systems. Symbols * and ° correspond to values found in experimental holdfasts.

A comparison of the gel content of pruned and control plants failed to reveal any significant differences (Fig. 4).

An analysis of the invertebrate colonies in pruned holdfasts showed no significant differences (Mann-Whitney U Test and Kolmogorov-Smirnov 2 Sample Test) between pruned discs and their control counterparts. This similarity was evident both in the morphometric ratios of the disc and in correlations between the disc and its fauna and the abundance, distribution and diversity of the latter.

b) Plants pruned at the first dichotomy:

A high mortality rate was also evident in the experimental group comprised of plants which lost all of their stipes at the first dichotomy. Figure 4 compares the length of time for which pruned plants and the control population remained on the beach. Three months into the experiment (August), the number of pruned plants began to decrease and plants disappeared from the beach, owing to a combination of factors. The stipe left behind when the portion above the first dichotomy is severed loses motility. In the months following, the stipes were filled with epiphytes which apparently slowed photosynthesis and ultimately caused the holdfast to shrink. With the apical portions of the plant gone, the stipes were also more vulnerable to prolonged attack by herbivorous snails and sea urchins (Tetrapygus niger), and the few apical portions capable of producing new fronds were destroyed. The longer the plant remained without regenerating stipes, the more the holdfast deteriorated, eventually losing its grip altogether and slipping off the rocks.

The gel content of the holdfasts of plants pruned at the first dichotomy is slightly but not significantly lower than that of the control plants. Such is not the case for the primary stipes, which have significantly more gel in pruned plants than in the controls.

An examination of the fauna in the holdfast discs also failed to reveal any significant differences from the control group. Hence, the data obtained for all holdfast/fauna relationships (Fig. 4) are within the range of variation of the standard discs.

To judge by the overall results of the two pruning systems tried, the complete plant should be extracted, because the regeneration capacity of the holdfasts and basal portions of the stipes is very slight if all stipes are severed. Furthermore, the attachment disc and basal parts of Lessonia nigrescens have the richest gel content. These pruning experiments also show that because the invertebrates housed in the holdfast are not affected by the severing of the erect portions of the plant, neither pruning system forces the animals to abandon their algal habitat. Finally, the disc should be removed when the plant is cut, to free up the substrate for juveniles of the same species.

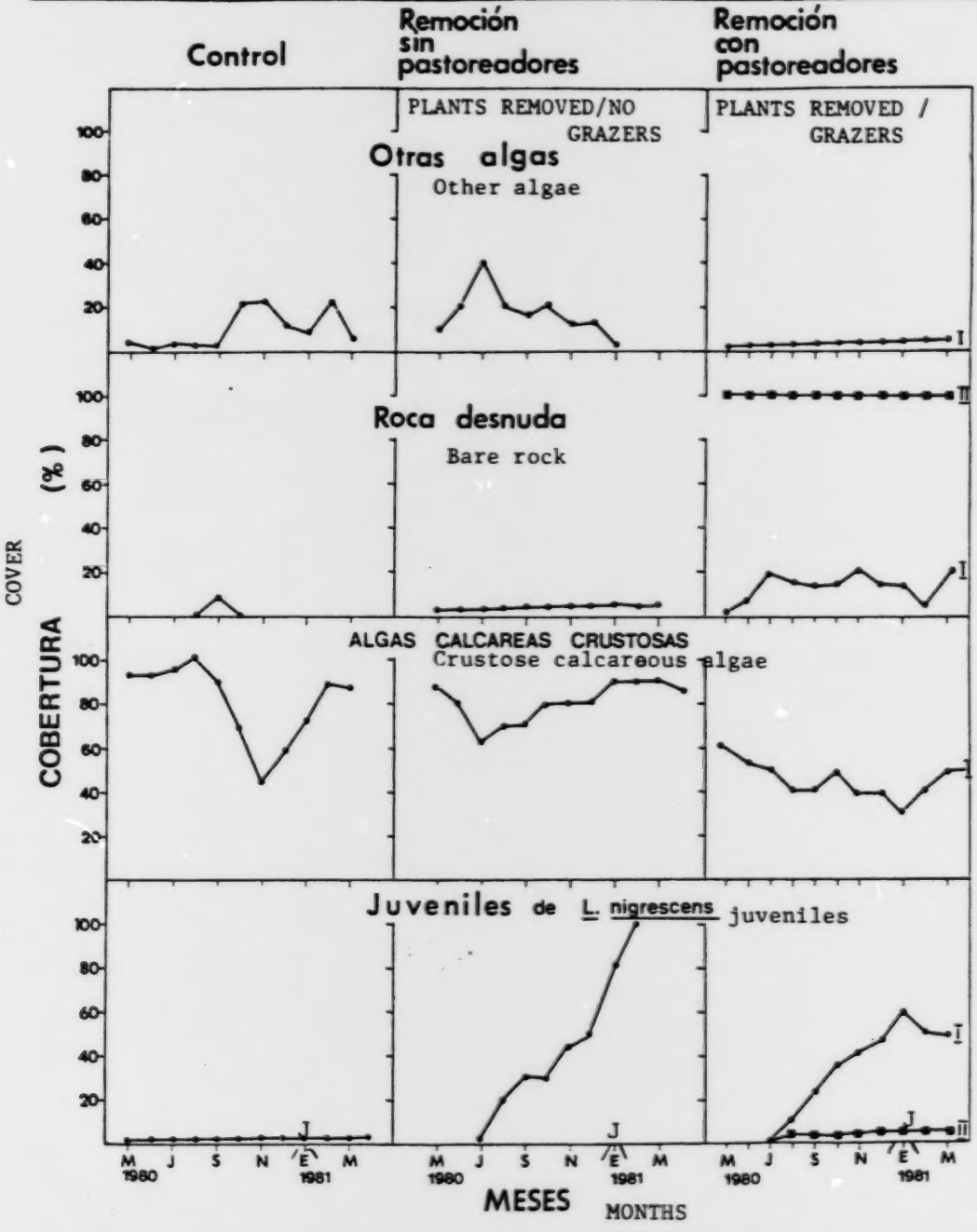


Figure 5.- Effect of removal of Lessonia nigrescens and invasion of grazers on juvenile settlement.

c) Removal of entire plants:

According to observations in the study areas in which adult Lessonia nigrescens plants were pruned 1-2 cm above the holdfast disc, the sea urchin Tetrapygus niger is capable of invading experimental plots, changing existing Lessonia nigrescens holdfast faunal communities, and deferring the settlement of Lessonia nigrescens juveniles. In order to analyze this influence in depth and predict the factors which might affect juvenile settlement, three experimental plots were prepared: one cleared of Lessonia nigrescens plants and grazers, one cleared of adult plants and stocked with grazers, and a third containing adult plants. As swaying adult Lessonia nigrescens fronds normally ward off sea urchins, a fourth experimental option (Lessonia nigrescens and Tetrapygus niger) was discarded.

The initial effect of the removal of L. nigrescens plants (Fig. 5) is a marked increase in the coverage of Gelidium filicinum and a reduction in Lithophyllum. When Lessonia nigrescens juveniles appear and the area eventually becomes more shaded, the percentage cover of G. felicinum lessens, and Lithophyllum becomes part of the second layer.

In the plot which had been cleared of adult Lessonia nigrescens plants and stocked with sea urchins (Tetrapygus niger), the layers of Lithophyllum, Ralfsia and Chthamalus diminished considerably (May, Fig. 5). At the same time, bare rock values increased from 0% in May to 25% the following months. Lessonia nigrescens juveniles began to settle there in August and gradually began to cover the substrate. This colonization started at the highest intertidal levels, and coverage of the lower levels owed more to the elongation of Lessonia nigrescens thalli than to settlement by new

plants. Hence, the bare rock values remained stable while Lessonia nigrescens juvenile cover values never reached 100%.

A comparison of these findings with the control plot (Fig. 5) shows Lessonia nigrescens juvenile settlement so sparse in the latter as to preclude any attempt at quantification. Adult plants of this species 148
continued to dominate, the sweeping motion of their fronds having inhibited the settlement and development of juvenile plants.

The potential for Lessonia nigrescens juvenile recruitment in any area which can be kept free of sea urchins by stipe movements of the surrounding plants suggested a final pruning experiment whereby plants were removed every 2 m and an empirical assessment was made of standard recruitment values for this species relative to the cleared space. It was thought that if the recruitment of Lessonia nigrescens is controlled naturally by the interference of adult plants and by grazers, then there must be an optimal interplant distance for natural recruitment. This distance should be a compromise between a very large clearance, which would be free of interference from adult plants but exposed to intense grazing, and a very small one with minimum grazing but maximum adult plant interference. Accordingly, the number of Lessonia nigrescens juveniles was calculated relative to interplant distance. The results shown in Fig. 6 leave no doubt that 1.5 - 2.0 m is the optimal distance between holdfasts for the recruitment of Lessonia nigrescens.

When juvenile settlement was compared in the four experimental plots (Fig. 7) (control site; no adult plants but sea urchins present; no adult

plants or sea urchins; thinned plants approximately 2 m apart), significant recruitment was recorded in only one of them (thinned plots). Several factors are at play here. The absence of Lessonia nigrescens juveniles in the experimental plot stocked with sea urchins can be explained by the effect of grazing on communities of marine algae. At the control site, juvenile settlement is limited by the presence of adult plants. In the plot cleared of both Lessonia nigrescens plants and grazers, the invasion of the substrate by other algae (Codium and Gelidium) was a significant deterrent to Lessonia nigrescens juvenile settlement. When plants are thinned leaving up to 2 m between individuals, juveniles of Lessonia nigrescens are free from interference by adult plants and safe from herbivorous grazers.

CONCLUSIONS

According to our research findings, the harvesting of Lessonia nigrescens can be properly managed if a number of basic biological features are taken into account. The overall production ecology data for this species suggest that:

a) Only plants with holdfast diameters exceeding 20 cm at the broadest point should be harvested. The estimated fresh weight of such plants is approximately 10 kg.

b) Harvesting should be restricted to the period from September to December.

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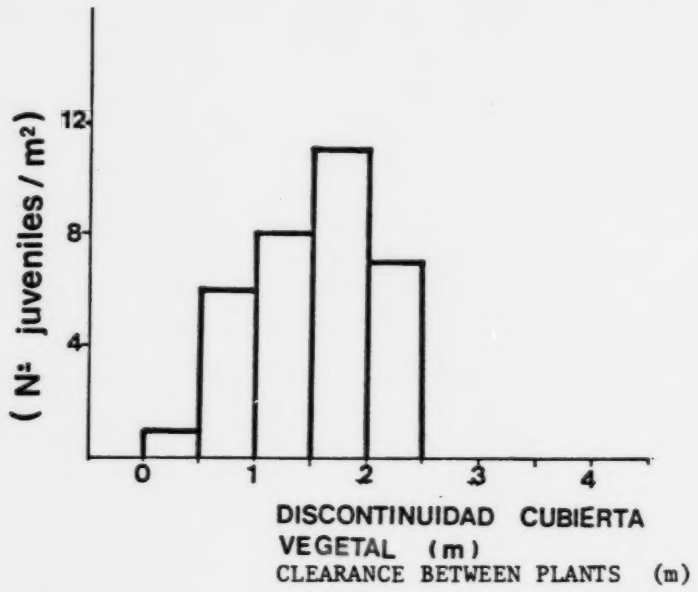

Figure 6.- Recruitment of Lessonia nigrescens juveniles and distance between holdfasts.

c) From an ecological standpoint, the entire plant should be removed from the intertidal system.

d) Optimal juvenile recruitment of Lessonia nigrescens will occur when the areas cleared of individuals of the species never exceed 2 m^2, measured as the distance from one holdfast to another. This would involve the removal of approximately 8 of every 12 plants at any given site.

Our findings for this species also suggest the need for similar research on other species of algae which play an important role in the economy.

(149)

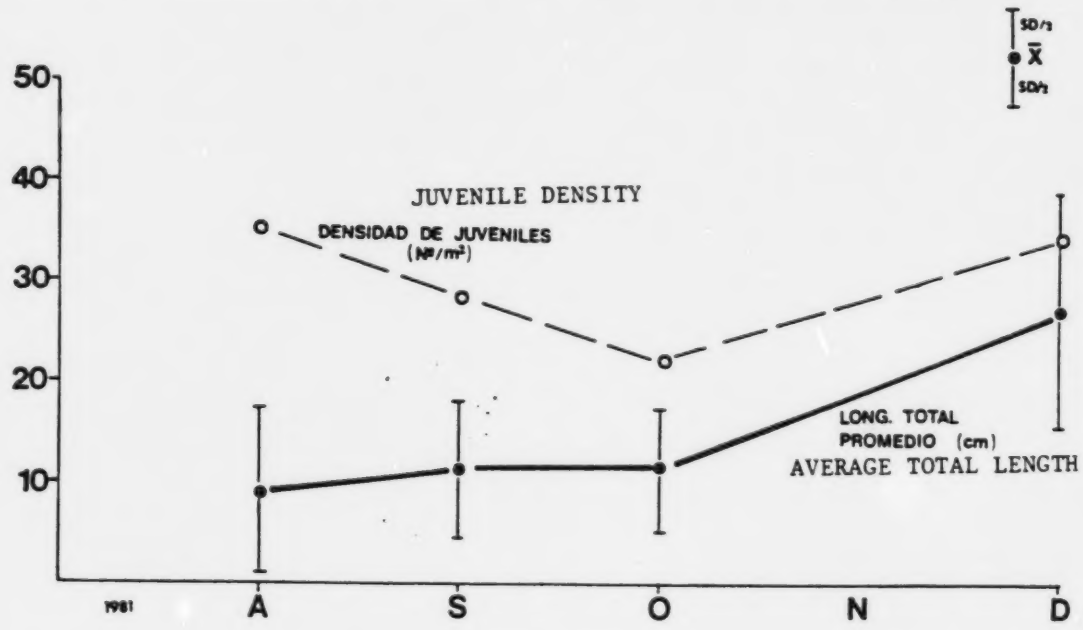

Figure 7.- Comparison of recruitment and elongation rate of juveniles in the four study areas cleared of L. nigrescens

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SUMMARY

The kelp *Lessonia nigrescens* (Phaeophyta, Laminariales) is the dominant organism as to cover and biomass in the intertidal - subtidal boundary of rocky exposed habitats along most temperate Pacific South America. The kelp is the habitat and determines the presence of a diverse number of invertebrates and other algae which occur within and between the kelp holdfasts. In addition, *L. nigrescens* is economically important in Chile as it is being annually exported as raw material for alginate production in amounts close to 6.000 tons of dry matter. This study reports results of a research program on production ecology of this species aimed to provide biological basis to handle the resource in Central Chile.

Results point to September - December as the best months to harvest this species in Central Chile. At this time of the year maximum growth and maximum fertility has already occurred while the adult plants show highest gel content. Juvenile settlement is maximum between August and November, ensuring substratum utilization by the same species after removal of the adult plants.

A combination of morphometric studies, measurements of growth rates, fertility and age together with studies of the structure of the invertebrate communities living in the holdfasts indicate individuals of about 20 cm. of maximum holdfasts diameter to be the minumum plant size to be removed. Holdfast diameter is a good estimator of most other morphometric and gravimetric relationships in this species. Plants with holdfasts diameters larger than 20 cm. have remained in the intertidal habitats long enough as to ensure reproduction at least during two seasons and have accumulated at least 10 Kilos of wet matter. Plants larger than this size are likely to be removed by water movement, thus having high probabilities of being lost by water movement.

Studies on spatial distribution of gel contents in the plant, evaluation of the regeneration capacity of several algal tissues and experimental testing of the removal effects of this species on other intertidal and subtidal algae and invertebrates advise to remove the plant completely during harvesting. Such a removal, however, should leave vegetational opening of less than 2 m. of inter-holdfast distance. The brushing effects of the fronds on the rocks at this size of vegetational discontinuity is small enough to allow increased juvenile recruitment but is large enough to limit invasion by large-sized grazers into the vegetational openings.

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